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BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities

Abbie S. A. Chapman[1] | Verena Tunnicliffe[2] | Amanda E. Bates[1,3]

[1]Ocean and Earth Science, University of Southampton Waterfront Campus, National Oceanography Centre, European Way, Southampton, UK

[2]Department of Biology and School of Earth and Ocean Sciences, University of Victoria, Victoria, BC, Canada

[3]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, NL, Canada

Correspondence
Abbie S. A. Chapman, Ocean and Earth Science, University of Southampton Waterfront Campus, National Oceanography Centre, European Way, Southampton, UK.
Email: asac1g09@soton.ac.uk

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Abstract

Aim: Rare species typically contribute more to functional diversity than common species. However, humans have altered the occupancy and abundance patterns of many species—the basis upon which we define "rarity." Here, we use a globally unique dataset from hydrothermal vents—an untouched ecosystem—to test whether rare species over-contribute to functional diversity.

Location: Juan de Fuca Ridge hydrothermal vent fields, Northeast Pacific Ocean.

Methods: We first conduct a comprehensive review to set up expectations for the relative contributions of rare and common species to functional diversity. We then quantify the rarity and commonness of 37 vent species with relevant trait information to assess the relationship between rarity and functional distinctiveness—a measure of the uniqueness of the traits of a species relative to traits of coexisting species. Next, we randomly assemble communities to test whether rare species over-contribute to functional diversity in artificial assemblages ranging in species richness. Then, we test whether biotic interactions influence functional diversity contributions by comparing the observed contribution of each species to a null expectation. Finally, we identify traits driving functional distinctiveness using a distance-based redundancy analysis.

Results: Across functional diversity metrics and species richness levels, we find that both rare and common species can contribute functional uniqueness. Some species always offer unique trait combinations, and these species host bacterial symbionts and provide habitat complexity. Moreover, we find that contributions of species to functional diversity may be influenced by biotic interactions.

Main conclusions: Our findings show that many common species make persistent, unique contributions to functional diversity. Thus, it is key to consider whether the abundance and occupancy of species have been reduced, relative to historical baselines, when interpreting the contributions of rare species to functional diversity. Our work highlights the importance of testing ecological theory in ecosystems unaffected by human activities for the conservation of biodiversity.

KEYWORDS

biological trait, conservation, diversity, functional distinctiveness, human impact, hydrothermal vent, rarity, review, species richness, unique trait combination

1 | INTRODUCTION

Rare species, in having small populations, restricted geographic ranges, and, often, narrow environmental niches are more vulnerable than common species to disturbance, environmental change, and competitive exclusion (Gaston, 1994; Rabinowitz, 1981). These rare species are often considered unique, endemic, and threatened—a combination that puts them at a higher risk of extinction than their common counterparts (Gaston, 1994, 2003; Gaston & Fuller, 2008; Hartley & Kunin, 2003; Margules & Pressey, 2000; Pimm, Jones, & Diamond, 1988). Yet, in possessing the characteristics that define rarity (low occupancy, abundance, and biomass), rare species may also contribute less than common species to ecosystem functioning processes (Grime, 1998; Smith & Knapp, 2003).

Functional traits are characteristics of a species affecting its contribution to the functioning of, and fitness within, an ecosystem (e.g., body size, trophic level). They can support empirical approaches when evaluating the respective roles of rare and common species in communities (Violle et al., 2017). Studies assessing the contributions of rare species to functional diversity encompass numerous methods, scales, and systems, which we comprehensively review in Table S1.1, provided in the Supporting Information. Seven of the eight studies that focus on contributions of rare species to functional diversity (Table S1.1) showed that rare species contributed more to functional diversity than expected given small abundances, occupancies, or ranges. Thus, the majority of evidence suggests that rare species contribute disproportionately to communities by offering functional uniqueness and, therefore, supporting diverse ecosystem functions (Bracken & Low, 2012; Ellingsen, Hewitt, & Thrush, 2007; Jain et al., 2014; Leitão et al., 2016; Mouillot et al., 2013; Smith & Knapp, 2003). Rare species introduce functional redundancy by sharing traits with other species (a phenomenon that becomes more likely as species richness increases) and, consequently, may provide insurance and resilience for an ecosystem under different, future environmental conditions (Jain et al., 2014; Mouillot et al., 2013; Walker, Kinzig, & Langridge, 1999; Yachi & Loreau, 1999).

Most studies reporting over-contribution of rare species to functional diversity focus on ecosystems that humans have fundamentally altered (e.g., through fishing and aquaculture, tourism, and logging), including coral reefs, rainforests, marine soft sediments, and alpine meadows (Mora et al., 2011; Vitousek, Mooney, Lubchenco, & Melillo, 1997; and see Table S1.1). By contrast, deep-sea hydrothermal vent communities thrive thousands of metres below the sea surface, without light, in warm, mineral-rich fluids that emerge from the seafloor. Vent systems support diverse microbial communities—the primary producers in this system—and fauna highly adapted to these environments (e.g., Figure 1c; Ramirez-Llodra et al., 2010). Energy in deep-ocean hydrothermal environments is provided via chemosynthesis,

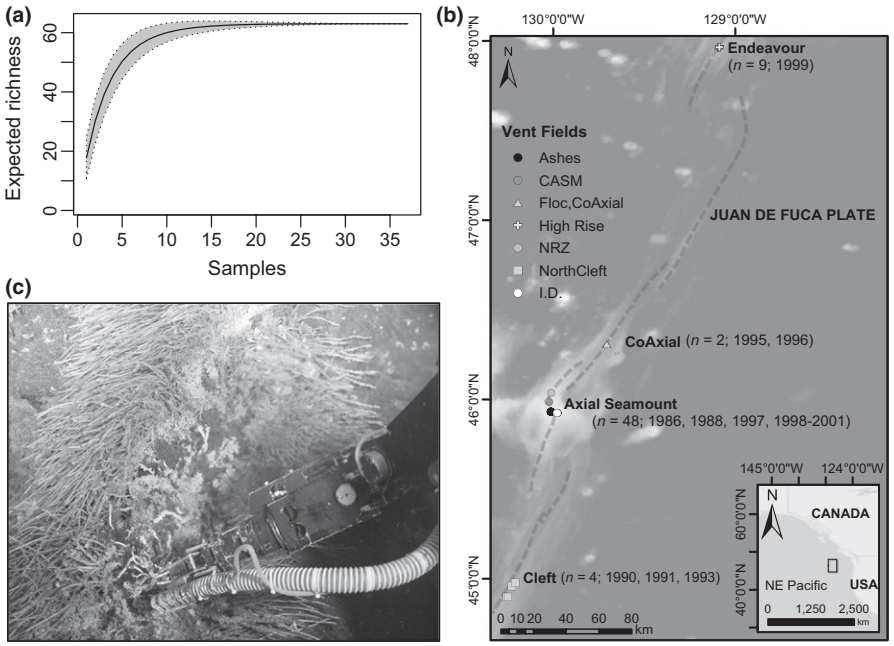

FIGURE 1 Overview of sampling effort and collection methods used to obtain macrofaunal data: (a) collector's curve (with 95% confidence intervals shown in grey) for the regional species pool compiled by combining all species sampled and using the Coleman, Mares, Willis, and Hsieh (1982) method; (b) location map, placing the hydrothermal vents ("sites") sampled along the Juan de Fuca Ridge (with "n" the number of vents sampled at a particular vent field (labelled in bold), preceding the years of sampling, and the ridge marked with dashed lines); (c) image showing tubeworm grab sampling with a submersible claw—a method commonly used to sample communities hosted by tubeworms like *Ridgeia piscesae*. The suction sample hose supplements the grab to retrieve animals on the substratum under the bushes, and mobile species escaping the grab. Image about 120 cm across. Bathymetry in (a) was sourced from Esri et al. (2012), vent field locations from sample records and the InterRidge Vents Database (Beaulieu, 2015; note that I.D. is International District), and the Juan de Fuca Ridge was drawn using information in Newman, Nedimović, Canales, and Carbotte (2011), Chadwick et al. (2013), and VanderBeek, Toomey, Hooft, and Wilcock (2016)

where microorganisms use the reduced compounds in vent fluid and inorganic carbon to form organic matter (e.g., Cavanaugh, McKiness, Newton, & Stewart, 2006 and Ramirez-Llodra et al., 2010). Hydrothermal vents therefore provide a rare opportunity to assess the relative contributions of rare and common species to functional diversity in a chemosynthetic environment with which only scientists have interacted, and thus human impacts are minimal, relative to terrestrial and shallow water systems (Ramirez-Llodra et al., 2011).

Here, we take advantage of a globally unique dataset of hydrothermal vent macrofaunal samples from one biogeographic region to test the hypothesis that rare species over-contribute to functional diversity. We focus on abundance, occupancy, and geographic extent as the main facets of rarity, in concordance with other rarity-oriented studies that use a functional trait approach, based on Rabinowitz' forms of rarity (Hartley & Kunin, 2003; Jain et al., 2014; Rabinowitz, 1981; Violle et al., 2017). We artificially assemble communities ranging in species richness from four to thirty-seven. For this range in species richness, we test the relative contribution of each species to local functional diversity in both artificially assembled and observed communities. Next, for the species that are functionally redundant with increasing species richness, we test whether species contributions differ from our null expectation as a result of community assembly processes. Finally, we identify the traits driving functional distinctiveness—a measure of the uniqueness of the trait values of a species, relative to the traits of all other species in a community (Grenié, Denelle, Tucker, Munoz, & Violle, 2017; Violle et al., 2017). Our work highlights differences in how species contribute to functional diversity in ecosystems that have not yet been reshaped by humans and, henceforth, a need to develop and test ecological theory in unaltered systems.

2 | METHODS

2.1 | Measuring rarity and commonness using abundance, occupancy, and geographic extent

This study focussed on invertebrate species assemblages ("communities") living more than 1,000 metres below the sea surface, at hydrothermal vents on basalt rocks along the Juan de Fuca Ridge tectonic plate boundary in the Northeast Pacific Ocean (Figure 1). Samples include sites in the Endeavour Marine Protected Area (Figure 1b). Sixty-three tubeworm samples (44 tubeworm grabs, 10 suction samples, and nine samples compiled from both) were taken from 47 basalt-hosted sites between 1986 and 2001 (as described in detail in: Marcus, Tunnicliffe, & Butterfield, 2009; Tsurumi & Tunnicliffe, 2001, 2003; Tunnicliffe et al., 1997; and Tunnicliffe, 2000). Based on these samples, and for each of 37 species, we quantified: (1) maximum relative abundance, to capture dominance potential and to discount sampling variability inherent in grab and suction samples (see Figure 1c); (2) occupancy (the number of samples within which a species occurred); and (3) geographic extent (the number of vent fields where each species occurred). We also computed a combined rarity index for each species (calculated as outlined in Leitão et al. (2016) but without log transformation), to enable cross-ecosystem comparability. The values for all four rarity metrics, for each of the 37 species, are provided in Table S1.2.

We include all macrofauna (≥1 mm in size) with species-level taxonomic identities and, thus, with fully assigned trait information (see species list in Table S1.2, verified using the World Register of Marine Species (Horton et al., 2017)). *Ridgeia piscesae* individuals (worms living inside tubes, aggregating to form bushes attached to the basalt rock substratum) were not included in this dataset, as they form the substratum for the sampled communities (e.g., see Figure 1c) in the same way that corals are often excluded from datasets as they provide habitat for reef fauna. The collector's curve in Figure 1a illustrates that sampling effort was sufficient to capture most of the Juan de Fuca Ridge vent species pool.

2.2 | Species traits

We assembled a matrix of species traits based on a comprehensive literature search and expert knowledge of these species (see Table S1.2). We selected five species-level traits that should reflect adaptations to rarity or commonness, as well as the functional contribution of a species to an ecosystem: relative adult mobility, maximum (recorded) body size, trophic level indicator, nutritional symbionts (present or absent), and forms a three-dimensional structure (yes or no). The justification and description of our traits are provided in Table S1.2.

2.3 | Testing whether rare species over-contribute to functional diversity in vent ecosystems

To test the hypothesis that rare species over-contribute to functional diversity, we compared the functional distinctiveness of each of the 37 species to their rarity (abundance, occupancy, geographic extent, and a combined rarity index). Functional distinctiveness was computed using the "funrar" and "cluster" packages in R (Grenié et al., 2017; Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017; R Core Team 2017; Violle et al., 2017). We also assessed whether functional distinctiveness was related to species richness, as functional diversity and taxonomic richness often have a strong linear relationship in other systems, detected using commonly used functional diversity metrics (e.g., functional richness—FRic, functional dispersion—FDis, and Rao's quadratic entropy (Laliberté, Legendre, & Shipley, 2014); see Figure S1.1). We then created artificial communities, applying a random subsampling approach, to test the hypothesis that rare species over-contribute to functional diversity in vent communities ranging from four species (the minimum observed species richness on the local scale) to 37 species (the maximum, regional-scale species pool). We assembled 1,000 communities per level of species richness (four to thirty-seven), sampling randomly without replacement to create a presence–absence matrix. This matrix was used to compute the proportion of artificially assembled communities within which each species would contribute a novel unique trait combination (UTC—i.e., the combination of traits a species possesses is not found in other species it coexists with; see equation overleaf); this proportion was plotted

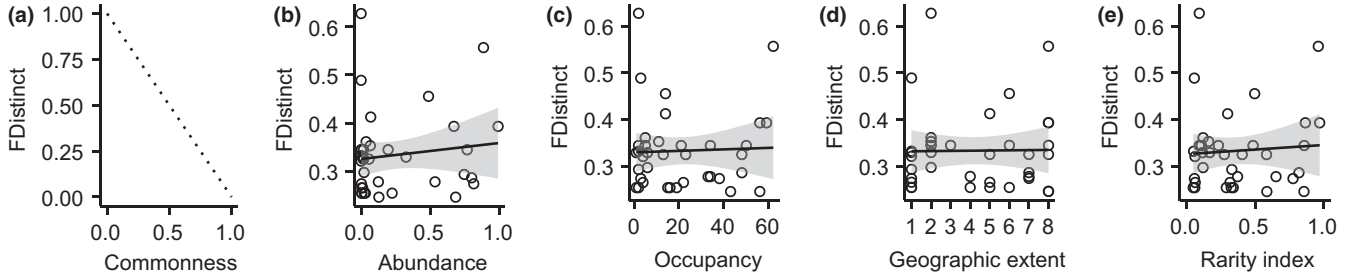

FIGURE 2 The relationship between rarity and functional distinctiveness in Juan de Fuca Ridge vent communities. (a) The expected linear relationship between rarity and distinctiveness, whereby more common species offer less functional distinctiveness than rare species. (b) The observed relationship between maximum relative abundance of each species and functional distinctiveness relative to all other species in the community. (c) The relationship between occupancy (number of samples within which the species occurs) and functional distinctiveness for each species. (d) The relationship between geographic extent (number of vent fields within which the species was observed) and functional distinctiveness of each species. (e) The relationship between the Rarity Index (per Leitão et al. (2016) without log transformation) and functional distinctiveness. Note that the relationships shown in (b), (c), (d) and (e) are relatively flat, contrary to the expectation presented in (a), suggesting that both rare and common species contribute functional distinctiveness. Model outputs to support panels (b), (c), (d) and (e) are provided in Table S1.4

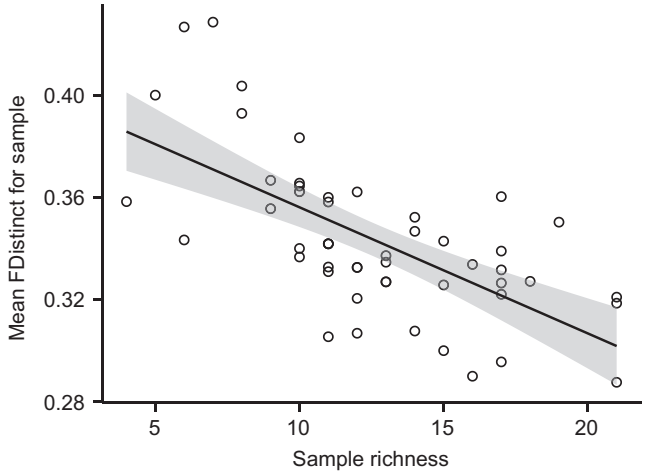

FIGURE 3 The relationship between taxonomic richness per sample and mean (across all species present in a sample) functional distinctiveness (FDistinct) per sample, as computed using the "distinctiveness" function of the "funrar" functional rarity package (Grenié et al., 2017). The linear relationship was fitted using a linear model (formula: mean FDistinct ~ richness) and is a significant linear relationship, with slope −0.005 and p-value <0.05 (adjusted R^2 value: 0.4157; F-statistic: 37.29 on 1 and 50 degrees of freedom)

against species richness using a LOESS line of best fit alongside the proportion calculated using observed (sampled) data (displayed as points). Supporting R (R Core Team, 2017) script is provided in Appendix S2. For the full set of N species, we calculate the proportion of communities (artificially assembled or sampled) within which a species i (i = 1, …, N) makes a unique trait combination contribution. This proportion, $p_{\text{species } i}$, is the number of UTCs in a community when species i is included ($\text{UTC}_{\text{total}}$) minus the number of UTCs when species i is excluded from the community (UTC_{-i}), divided by the total number of communities species i is present in, C:

$$p_{\text{species } i} = \frac{\Sigma\left(\text{UTC}_{\text{total}} - \text{UTC}_{-i}\right)}{C}.$$

We used the Unique Trait Combination (UTC) metric to quantify species contributions to functional diversity to capture the redundancy and uniqueness of combinations of traits from a multifunctional perspective. This approach was selected as Mouillot et al. (2013) show that species with distinct trait combinations are more likely to support vulnerable ecosystem functions than species with commonly observed trait combinations. The UTC metric was computed using the "mvfd" function of the "multirich" R package (Keyel & Wiegand, 2016; R Core Team, 2017). This metric does not share limitations with the commonly used convex-hull-based "FRic" functional richness metric (of particular relevance, given the low richness of vent communities; Cornwell, Schwilk, & Ackerly, 2006; Laliberté et al., 2014; Schmera, Podani, & Erős, 2009; Villéger, Mason, & Mouillot, 2008); the UTC metric can accommodate the limited number of continuous measurements available for relatively inaccessible and expensive to sample deep-sea hydrothermal vent species by incorporating categorical trait values (Keyel & Wiegand, 2016).

Species were placed in one of three groups ("always unique," "redundant with richness", or "rapidly redundant") according to the shape of the relationship between species richness and the proportion of communities within which their trait combination was unique in 1,000 randomly assembled artificial communities. We tested whether community assembly processes and biotic interactions could be shaping the functional uniqueness of the species that we identified as becoming increasingly redundant with richness (for species observed in at least 10 samples—an arbitrary threshold selected to minimize sampling effort bias). We compared the proportion of sampled communities in which each of the species in the "redundant with richness" group observed in at least 10 samples contributed a UTC to a null expectation established using our randomly assembled community data. We used a binomial test to determine whether the proportion contributed by sampled species differed significantly from the proportion species would be expected to contribute based on the outcomes of the randomly assembled samples. Richness levels were binned for the tests as, despite using one of the world's most

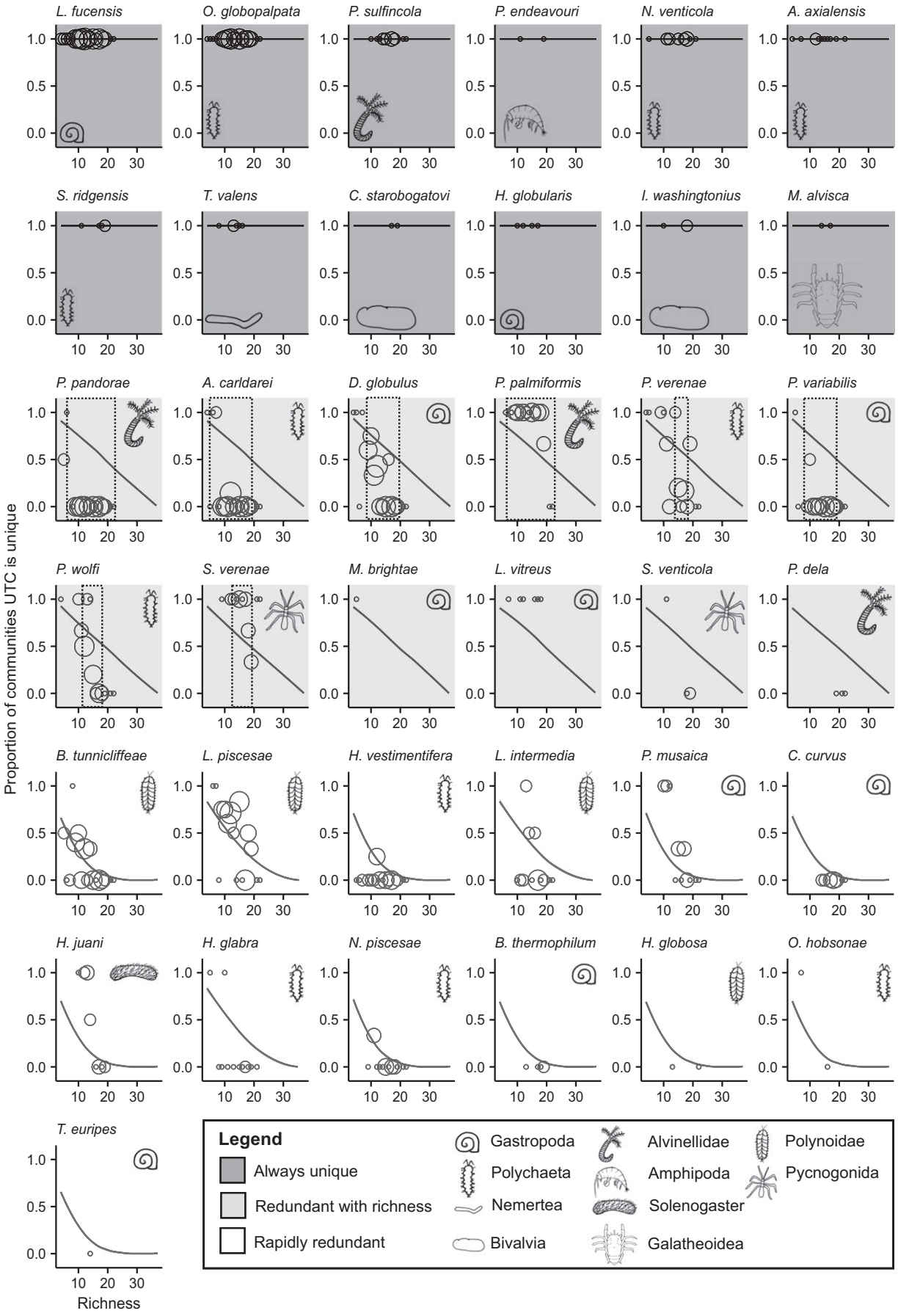
L. fucensis
O. globopalpata
P. sulfincola
P. endeavouri
N. venticola
A. axialensis
S. ridgensis
T. valens
C. starobogatovi
H. globularis
I. washingtonius
M. alvisca
P. pandorae
A. carldarei
D. globulus
P. palmiformis
P. verenae
P. variabilis
P. wolfi
S. verenae
M. brightae
L. vitreus
S. venticola
P. dela
B. tunnicliffeae
L. piscesae
H. vestimentifera
L. intermedia
P. musaica
C. curvus
H. juani
H. glabra
N. piscesae
B. thermophilum
H. globosa
O. hobsonae
T. euripes
Proportion of communities UTC is unique
Richness
Legend
Always unique
Redundant with richness
Rapidly redundant
Gastropoda
Polychaeta
Nemertea
Bivalvia
Alvinellidae
Amphipoda
Solenogaster
Galatheoidea
Polynoidae
Pycnogonida

FIGURE 4 The proportion of communities within which each species makes a unique trait combination (UTC) contribution. Each panel in this Figure shows the proportion of communities to which a species (named at the top of each panel) makes a unique contribution (*y*-axis), relative to species richness (*x*-axis). Solid lines in each panel depict the relationships identified using artificial, randomly assembled communities of four to thirty-seven species in richness (mean values based on communities that were randomly assembled 1,000 times per level of richness—see Section 2.3). Circles in each panel are observations from sample data, with circle size relative to the number of samples with the given result. Dotted boxes, shown on some central panels, encompass the richness bins used in the binomial tests to see whether the observed UTC contribution made by a species significantly differed from the null, random expectation (shown in the artificial community line). Each panel is shaded according to the groups listed in the legend that are assigned based on the shape of the relationship between species richness and UTC contributions revealed in the randomly assembled communities. Cartoon inserts illustrate the taxonomic group of each species, as outlined in the Legend. Species names have been shortened, but are given in full in Table S1.2. The species presented on this Figure combine to represent the regional species pool—the 37 taxa identified to species level for basalt samples from the Juan de Fuca Ridge

complete hydrothermal vent sample datasets, we had insufficient samples to conduct the test for each richness level. Bins are highlighted as dotted boxes in Figure 4 (with further details and binomial test results presented in Table S1.3). We selected the minimum probability value for the null expectation in each bin to be conservative.

Finally, to assess the trait similarity among the species in the "always unique" group, we used a distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999). We adapted the db-RDA with an input of a species by trait matrix as our explanatory matrix and a species by functional distinctiveness matrix as our response. Given the nature of our functional trait data (i.e., some semi-quantitative traits), we used the Gower distance metric for the db-RDA (Gower & Legendre, 1986; Laliberté & Legendre, 2010). The db-RDA is appropriate because our data did not meet assumptions of Euclidean distances and normality (Legendre & Anderson, 1999; Legendre & Legendre, 1998).

3 | RESULTS

In 63 hydrothermal vent community samples, 27 species were relatively rare (if we consider a species with a rarity index value of <0.5 to be rare, as the index is scaled from 0 to 1; Figure S1.2) and 10 relatively common (>0.5 rarity index value; Figure S1.2). In these 63 samples, some of the most rare and common species contributed to functional distinctiveness. All three measures of rarity, as well as a combined rarity index, hold the same flat relationship with distinctiveness (Figure 2); therefore, this outcome does not support a hypothesis of increasing contribution with rarity (Figure 2a; Table S1.4 contains the outputs of the linear models presented in Figure 2b–e). Nonetheless, as species richness increased in sampled communities, functional distinctiveness decreased (Figure 3), supporting the expected pattern of increasing functional redundancy with richness; when the number of species increases, the probability of a new species contributing to functional distinctiveness decreases because there is a higher chance that the traits of a new species already exist in another species in the community. These results were not simply an outcome of trait selection or scoring methodology, as tested and discussed in Appendices S3 and S4.

Given the strong relationship between species richness and functional distinctiveness, we further tested whether rare and common species both contribute to functional distinctiveness across a range of species richness levels, spanning beyond the maximum sample richness (21) to that of the regional pool (37). We accounted for the contributions made by species given known co-occurrences, rather than contributions to the overall regional pool—which can include species that, in reality, never co-occur. Considering the independent contributions of each species (Figure 4), we found that 12 species, including eight rare and two very common species, contributed unique trait combinations at all levels of richness ("always unique"). Twelve species contributed uniqueness at low levels of richness but became increasingly redundant with richness ("redundant with richness"), while 13 became rapidly redundant at lower richness ("rapidly redundant"). For the most part, the groupings highlighted in Figure 4 comprised a mix of taxonomic classes, but all the scaleworm polychaetes (in the phylum Annelida) fell only within the "rapidly redundant" group. Each group is described in more detail in Table S1.5.

The proportion of communities in which eight, well-sampled species in the "redundant with richness" group made unique contributions to the assemblages in which they were sampled was compared to the random expectation. The worms, *Paralvinella pandorae* and *Amphisamytha carldarei*, and snails, *Depressigyra globulus* and *Provanna variabilis*, contributed a unique trait combination (UTC) in fewer communities than would be expected by chance (Figure 4 and Table S1.3). By contrast, the worm, *Paralvinella palmiformis*, and sea spider, *Sericosura verenae*, contributed a UTC in more communities than expected (Figure 4 and Table S1.3). The contributions of two worms, *Protomystides verenae* and *Parougia wolfi*, did not differ significantly from random (see Table S1.3).

Two key traits emerged as driving functional distinctiveness in the "always unique" group: hosting nutritional symbionts and forming a three-dimensional structure (Figure 5, and see Table S1.6). These two traits also shaped the functional distinctiveness of species in the "redundant with richness" and "rapidly redundant" groups, influencing the relative distances between all species (Tables S1.5 and S1.6). The direction of influence differs in these traits for species in the "rapidly redundant" group, though, as these species do not form 3D structures or have nutritional symbionts (Table S1.5).

4 | DISCUSSION

Here, we show that rare species do not contribute significantly more to the functional distinctiveness of vent communities than more common species. This finding is supported at all levels of species

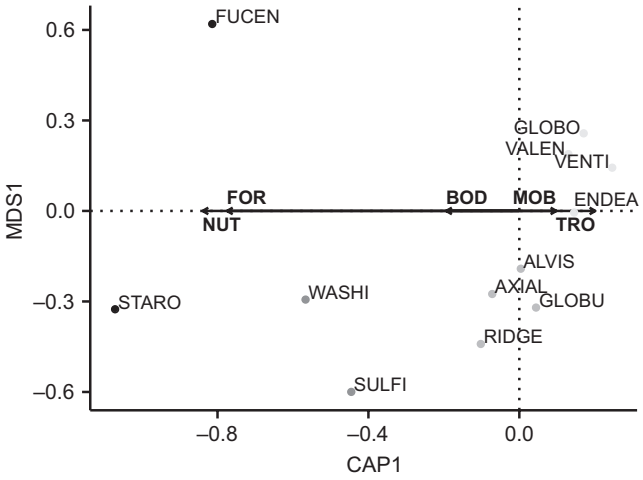

FIGURE 5 Distance-based redundancy analysis (db-RDA) of Gower distances showing the functional distinctiveness of each of the species relative to one another and the potential traits driving distinctiveness differences (labelled in bold next to arrows, with trait names shortened as follows: NUT—nutritional symbionts, FOR—forms a 3D structure, BOD—maximum body size (mm), MOB—relative adult mobility, and TRO—trophic level indicator). "Nutritional Symbionts" and "Forms a 3D Structure" were significant traits in the db-RDA model, based on an ANOVA by terms with 200 permutations (a permutation test used to assess the significance of constraints for each trait separately (Oksanen et al., 2017); see Table S1.6). Functional distinctiveness is colour coded, with the two most functionally distinct species (*Lepetodrilus fucensis* and *Calyptogena starobogatovi*) shown in black and the point colours becoming lighter with decreasing functional distinctiveness. The species labelled on this plot belong to the "always unique" group (see Figure 4), although the functional distinctiveness of all 37 species was driven by the same traits. Species names shortened in this Figure are: ALVIS—*Munidopsis alvisca*, AXIAL—*Amphiduropsis axialensis*, ENDEA—*Pardalisca endeavouri*, FUCEN—*Lepetodrilus fucensis*, GLOBO—*Ophryotrocha globopalpata*, GLOBU—*Hyalogyrina globularis*, RIDGE—*Sphaerosyllis ridgensis*, STARO—*Calyptogena starobogatovi*, SULFI—*Paralvinella sulfincola*, VALEN—*Thermanemertes valens*, VENTI—*Sericosura venticola* and WASHI—*Idas washingtonius*

richness (from the minimum sampled richness—four species—to the 37 species regional pool). Our results contradict those of most research into rarity-functional diversity relationships to date, which, instead, demonstrate that rare species over-contribute to functional diversity (a review of the research on this topic is presented in Table S1.1). For example, in coral reefs, tropical rainforests, and alpine meadows, the most distinct trait combinations are supported by rare species (Mouillot et al., 2013). In addition, in a removal experiment conducted on a rocky shore community, rare species had bottom-up influences on the diversity and abundance of consumers (Bracken & Low, 2012).

Despite diverging from the expectation set in other trait-based studies, our findings are supported by ecological theory. If rare species are specialists, adapted to specific environmental conditions (hence their small geographic range, for example), we expect rarer species to have traits that reflect this specialization. These specialist traits would be dissimilar to the traits of species occupying other habitats and niches, enabling specialist rare species to persist with low occupancy and abundance (Gaston, 1994; Rabinowitz, 1981). At the same time, common species are expected to thrive in a wider range of habitats and environmental conditions, and have more generalist traits enabling them to do so; yet, common species must also possess unique traits (or combinations of traits) to successfully outcompete other species for space and resources, attain high abundances, maintain broad geographic ranges, and occupy many habitats (Gaston, 2010, 2011; Tilman, 1999).

While our results are supported by ecological theory, there remain several explanations as to why our results differ from previous studies. These include: (1) sampling method (i.e., at vents, remotely operated equipment enables the retrieval of intact assemblages comprising diverse taxa, rather than the taxon-specific "community" data collected for some studies described in Table S1.1); (2) trait selection (e.g., see Lefcheck, Bastazini, & Griffin, 2014) and scoring methodology (as the number of modalities per trait can influence trait space and, thus, indices computed using a multidimensional trait space volume; Lefcheck et al., 2014); (3) species richness of the study system, which can shape functional diversity by influencing the potential for functional redundancy; and (4) the natural and anthropogenic processes affecting ecosystem stability and function. We discuss these possible explanations in more detail in Appendix S3 and argue (with support in Appendix S4) why each was unlikely to explain the novel result that common species can contribute to functional diversity.

After considering alternative explanations, we propose that our results may, instead, differ from the expectation set in shallow marine and terrestrial ecosystems because vents are unique in being a relatively untouched ecosystem on Earth. Species abundance and occupancy patterns at vents have not yet been markedly altered by human activities (Ramirez-Llodra et al., 2011). For example, Juan de Fuca Ridge predator species *Buccinum thermophilum*, a snail, and *Nereis piscesae*, a worm, are redundant (in terms of the traits we selected) with other species in nearly every community in which they occur. It is likely that relatively large predatory species like these would be unique if incorporated in trait-based studies of ecosystems within which humans have removed many large, mobile predators (e.g., by hunting). Conversely, in Juan de Fuca vent communities, we find many relatively large predators that are mobile and carnivorous (Bergquist et al., 2007; Kelly, Metaxas, & Butterfield, 2007), making these traits—and thus these snail and worm species—functionally redundant in these systems.

At vents and in other remote ecosystems, rarity and commonness are the result of various abiotic and biotic processes shaping abundance, occupancy, and geographic range extent. In contrast, in ecosystems such as coral reefs and tropical rainforests, human activities have caused species losses and gains, and have fundamentally altered species abundances, occupancies, and geographic range dimensions (e.g., see Inger et al., 2015). Thus, when we study "rare" species in human-altered systems, we might be including species that were once common but appear low in abundance, extent, or occupancy at the time of study as a result of human action (Gaston, 2008; Gaston & Fuller, 2008); this would affect our perceived contributions of "rare"

species to functional diversity. For example, *Dipturus batis* (common skate) is a demersal marine species that has been reduced in number by human activities (Gaston & Fuller, 2008) and would be considered "rare" if studied today, as opposed to several decades prior.

It could therefore be argued that ecological research more widely would benefit from studying undisturbed systems like hydrothermal vents, as results such as those presented here have conservation and management implications. Rare species are often the focus of conservation strategies because they may be more prone to extinction (e.g., a species low in abundance could be lost altogether with the loss of several individuals; Gaston, 1994; Kruckeberg & Rabinowitz, 1985; Margules & Pressey, 2000). However, we have shown that common species also influence functional diversity in vent systems; thus, common species losses may also have important implications for ecosystem functioning and stability (e.g., see Lyons, Brigham, Traut, & Schwartz, 2005 and Tilman et al., 1997 for discussions of relationships between functional diversity and ecosystem functioning). For instance, if a common species facilitates a rare species, reducing the number of individuals of this common species will likely have a knock-on effect on the rare species (Gaston, 2011; Lindenmayer et al., 2011). For hydrothermal vent communities specifically, as deep-sea mining is likely to affect these presently undisturbed assemblages, conservation approaches must move rapidly to assess effects of species loss (Van Dover et al., 2017). Given our findings at the Juan de Fuca Ridge, we propose that conservation planning incorporating functional assessments that include the roles of common species may be particularly effective at vents, as well as in other ecosystems, where rare species are more often the focus at present.

Furthermore, our work advances understanding of the ecology of hydrothermal vent communities in identifying features of these communities that clarify assemblage structures and key species roles (summarized in Table S1.7). We identify two traits underpinning contributions to relative functional distinctiveness: "possessing nutritional symbionts" and "forming a three-dimensional (3D) structure." Possessing nutritional, bacterial symbionts enables a host species to access chemical energy and accumulate biomass in the same way that corals rely on zooxanthellae to reach high biomass in a low-productivity tropical ocean. Common species hosting nutritional symbionts will have direct access to primary productivity (Cavanaugh et al., 2006; Stewart, Newton, & Cavanaugh, 2005), and, as space can be limited at vents, this often translates to increased abundance and biomass. At the same time, rare species might also benefit from hosting nutritional symbionts, to thrive with limited resources or compete with common species, especially if the symbiont-host association requires conditions that differ from competitive dominants.

In addition to, or instead of, having nutritional symbionts, for some vent species that have limited access to tolerable conditions in high temperature or fluid flux gradients, the ability to form 3D structures may enable them to modulate flow and/or access specific habitats (Bates, Lee, Tunnicliffe, & Lamare, 2010; Bates, Tunnicliffe, & Lee, 2005; Kelly & Metaxas, 2008; Tsurumi & Tunnicliffe, 2003). Common *Lepetodrilus fucensis* limpets access and alter fluid flow patterns by stacking vertically (see Bates et al., 2005), like epiphytes on forest trees. Such species that form 3D structures likely also play a key role as ecosystem engineers, increasing habitat complexity and facilitating colonization by other species. In other ecosystems, common species are typically the engineers (Gaston, 2011). Also common are the limpets and tube-forming polychaetes that form 3D structures at Juan de Fuca Ridge vents, enabling other species to colonize the augmented surface area. Their structures can modify local fluid flow patterns and provide surfaces for microbial colonization, thereby increasing food resources for grazers. Additionally, the functionally distinct rare species that form 3D structures potentially act as "cornerstone species" in small and limited niches, playing an important role in structuring the local space (as defined and observed in rocky intertidal communities in Bracken & Low, 2012). For example, the most distinct rare species (bivalves *Calyptogena starobogatovi* and *Idas washingtonius*) usually inhabit other chemosynthetic environments; but, in our tubeworm bush samples, their shells provide stable habitats for settlers of other species, even when the bivalves themselves are no longer alive.

Coexistence theory helps to explain the unique trait combination (UTC) contributions of these vent species. Kraft, Valencia, and Ackerly (2008) tested coexistence theories (e.g., neutral and niche-based models) in Amazonian forest trees using functional traits. They compared measures of community-trait structure to a null expectation of random assembly, with habitat filtering deemed to be taking place if the range of observed trait values was smaller than that of randomly assembled communities. In our study, the bristle worm *Paralvinella pandorae* offered a redundant trait combination more times than expected based on random assembly; the opposite was true for its congener, *Paralvinella palmiformis*. Indeed, these two alvinellid worms are competitors, with *Paralvinella pandorae* the inferior competitor because of its narrower trophic and space requirements (Levesque, Juniper, & Marcus, 2003; Marcus et al., 2009; Tunnicliffe et al., 1997). Meanwhile, the worm, *Amphisamytha carldarei*, and snails, *Depressigyra globulus* and *Provanna variabilis*, make unique contributions to significantly fewer communities than we would expect by chance. The contributions of these species might, therefore, be affected by habitat filtering (in addition to, or instead of, competitive interactions). In contrast, the sea spider, *Sericosura verenae*, makes a unique contribution in more communities than in the null expectation, so its contributions might be affected by niche differentiation.

We used a novel approach to test whether the proportion of communities each species contributed a UTC to was significantly different from a random expectation. Trait-based studies of rarity and functional diversity have previously used a regional pool-based approach, thereby incorporating species that, in reality, never co-occur. Our method may, in cases with representative sampling, provide a tool to identify species that are limited in functional distinctiveness by other co-occurring species. Thus, our approach could be used to test for community assembly mechanisms—a common goal in trait-based ecology (Ackerly & Cornwell, 2007; de Bello, 2012; de Bello et al., 2012)—alongside analyses of other influential processes, such as larval dispersal, colonization, and suitability of the abiotic environment (Kraft et al., 2015; MacArthur & Levins, 1967). Our approach could also prove a useful ecological tool for investigating more general relationships between

rarity, species richness, functional distinctiveness, and co-occurrence patterns in communities.

In conclusion, our understanding of many ecological processes, biodiversity patterns, and resilience are based on systems that are significantly altered by human activities. Using sampled and artificial (randomly assembled) hydrothermal vent communities, we show that rare and common species both offer functional distinctiveness, with contributions of species shaped by traits important for chemosynthesis, ecosystem engineering, and physico-chemical tolerance. Furthermore, functional uniqueness can be constrained by biotic interactions, such as competition, habitat filtering, and niche differentiation. Our findings offer new perspectives on rarity, commonness, distinctiveness, and redundancy; thus, we suggest that hydrothermal vent habitats and other relatively untouched environments offer unique windows into ecology, conservation, and biodiversity theory. Ultimately, here, we highlight a need to test ecological hypotheses in Earth's remaining untouched systems, to facilitate our ecological understanding of the systems that we, as humans, have already altered.

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DATA ACCESSIBILITY

The data supporting the results are provided in the Supporting Information.

ORCID

Abbie S. A. Chapman http://orcid.org/0000-0002-7812-2046

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BIOSKETCHES

Abbie Chapman is a PhD Candidate at the University of Southampton (www.abbiechapman.com). She is researching the biodiversity of hydrothermal vents across the globe using a functional trait approach and is co-PI (with Amanda Bates) of the "sFDvent" working group, building the first global functional trait database for vent species. Verena Tunnicliffe is a Canada Research Chair in Deep Ocean Research based at the University of Victoria. Verena focuses on the characteristics that enable populations to survive in extreme habitats and primarily researches deep-sea ecosystems such as hydrothermal vents and submarine volcanoes. Amanda Bates' research quantifies biodiversity in time and space and relates emergent patterns to environmental drivers and physiological tolerances of species. Her aim is to transform physiological data into predictive tools that incorporate both exposure and species' sensitivities to global change drivers. In doing so, she generates novel theories and approaches for managing and conserving marine living resources.

Author contributions: ASAC and AEB designed the study; VT provided sample data; all authors contributed trait data; ASAC and AEB undertook the analyses, with outcomes verified by VT; ASAC drafted the manuscript; and all authors contributed substantially to revisions.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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